

# The taxonomic and conservation status of the *Oxygogon* helmetcrests

## *Taxonomia y estado de conservacion de Oxygogon guerinii*

Nigel J. Collar<sup>1</sup> & Paul Salaman<sup>2</sup>

<sup>1</sup>BirdLife International, Girton Road, Cambridge CB3 0NA; and Bird Group, Department of Life Sciences, Natural History Museum, Akeman St, Tring, Herts HP23 6AP, UK. Email: [nigel.collar@birdlife.org](mailto:nigel.collar@birdlife.org)

<sup>2</sup>Rainforest Trust, 25 Horner Street, Warrenton VA 20186, USA. Email: [paul@RainforestTrust.org](mailto:paul@RainforestTrust.org)

### Abstract

Morphological variation in the genus *Oxygogon* was studied using biometrics and plumage data, and available sound recordings were inspected. Four distinct populations of Bearded Helmetcrest *Oxygogon guerinii* (*cyanolaemus* in the Sierra Nevada de Santa Marta, *lindenii* in the Venezuelan Andes, *guerinii* in the East Andes of Colombia, and *stubelii* in the Central Andes of Colombia) were lumped without justification in the 1940s but are highly distinct in multiple plumage and morphometric characters. Species rank is suggested for all four taxa, following species scoring tests. We draw special attention to *O. cyanolaemus* of the Sierra Nevada de Santa Marta, which has not been reported since 1946. It is recommended for the IUCN criteria of Critically Endangered, although it may possibly already be extinct.

**Key words:** *Oxygogon*, Bearded helmetcrests, taxonomy, conservation, Sierra Nevada de Santa Marta, paramo

### Resumen

Se estudió la variación morfológica en el género *Oxygogon*, utilizando datos sobre biometría y plumaje, además fueron estudiadas grabaciones de vocalizaciones. Cuatro poblaciones distintas de *Oxygogon guerinii* (*cyanolaemus* en la Sierra Nevada de Santa Marta, *lindenii* en los Andes venezolanos, *guerinii* en los Andes del este de Colombia, y *stubelii* en los Andes Centrales de Colombia), fueron fusionadas sin justificación en la década de 1940, pero son bastante distintas en muchas características de plumaje y morfometría. Se sugiere asignar estatus de especie a cada uno de ellas, utilizando un sistema de puntuación de especies. Llamamos la atención en particular a la especie *O. cyanolaemus* de la Sierra Nevada de Santa Marta, que no se ha reportado desde 1946. Se recomienda para el estatus de UICN En Peligro Crítico, aunque posiblemente, podía estar extinta.

**Palabras clave:** *Oxygogon*, Chivos de páramo, taxonomía, conservación, Sierra Nevada de Santa Marta, páramo.

### Introduction

Bearded Helmetcrest *Oxygogon guerinii* is a hummingbird comprising four taxonomically distinct populations, named as follows: *cyanolaemus* in the Sierra Nevada de Santa Marta (Colombia), *lindenii* in the Venezuelan Andes, *guerinii* in the East Andes of Colombia south to Cundinamarca, and *stubelii* (spelling here in accordance with Dickinson & Remsen 2013) in the Central Andes of Colombia. These four taxa were originally described as separate species by Boissonneau (1840: *guerinii*), Parzudaki (1845: *lindenii*), Salvin & Godman (1880: *cyanolaemus*) and Meyer (1884: *stubelii*). Species rank for all recognised taxa was afforded by the early pioneers of hummingbird taxonomy, such as Gould (1887), Boucard (1896) and Hartert (1900), followed by Cory (1918). However, these four taxa were then lumped into a single species by Peters (1945), and for almost 70 years Peters's treatment has been universally followed (e.g. Meyer de Schauensee 1948 1952, 1966, Morony *et al.* 1975, Wolters 1975 1982, Hilty & Brown 1986, Fjeldså & Krabbe 1990, Sibley & Monroe 1990, Clements 1991, 2000, 2007, Monroe & Sibley 1993, Stotz *et al.* 1996, Züchner 1999, Dickinson 2003, Hilty 2003, Gill & Wright 2006, Restall *et al.* 2006, McMullan *et al.* 2010, Dickinson & Remsen 2013).

*Oxygogon* is confined to montane habitats, specifically paramo, subparamo and adjacent elfin forest ecotones, and has a strong association with *Espeletia* (Hilty & Brown 1986, Züchner 1999, Hilty 2003, Restall *et al.* 2006, Salamanca-Reyes 2011), locally known as 'frailejones', a distinctive genus of plants in the subtribe Espeletiinae endemic to and locally abundant in the high Andean paramos of Venezuela, Colombia and northernmost Ecuador (Rauscher 2002). The literature indicates elevations of 3,200–5,200 m in Colombia (Hilty & Brown 1986) and 3,600–4,500 m (with a sight record from 2,800 m) in Venezuela (Hilty 2003), with 3,200–4,500 m as an overall generalisation (Stotz *et al.* 1996). Inevitably, therefore, each of these taxa, although grouped relatively closely in north-western South America, must have been isolated for considerable lengths of time. Paramo evolved during the Late Pliocene or Early Pleistocene (2–4 million years ago) during the final uplift of the Andes (van der Hammen & Cleef 1986). During the latter part of the Quaternary of the last glacial stadial, there were numerous changes in the elevational limits of paramo and forest, with paramo periodically covering a much greater area and descending to 2,000 m (van der Hammen & Cleef 1986), although the Magdalena valley was a major barrier between the East Andes, Central Andes and Sierra Nevada de Santa Marta.

The paramos and avifaunas of the East Andes, Central Andes, Venezuelan Andes and Santa Marta are each separated by at least 150 km (*guerinii* and *stubelii*) and up to 350 km (*cyanolaemus* and *lindenii*) of different (lower-elevation) habitats, resulting in each of them having several unique elements and being treated as separate 'Endemic Bird Areas' (Stattersfield *et al.* 1998).

Only two recent publications illustrate the four taxa in *Oxygogon* together, namely del Hoyo *et al.* (1999) and Restall *et al.* (2006). From these and from the accompanying textual descriptions (credited in the former to Züchner 1999) it is apparent that each form is highly distinctive, and indeed Züchner (1999) remarked: 'Based on morphological differences, the races could be considered four separate species'. This point was picked up in a footnote ('May consist of more than one species') by Dickinson & Remsen (2013), but otherwise there appears to have been no expression of interest in the issue of species limits within the genus. At the same time, it came to our attention that the Santa Marta population is rare and has gone unrecorded for decades. This genus therefore emerged as a priority for taxonomic review. Here we consider the morphological differences afresh, and at the same time assemble what evidence we can find relating to the conservation status of each taxon.

## Methods

To investigate the taxonomic status of each taxon of *Oxygogon* we examined specimens in the American Museum of Natural History (AMNH), New York; the Natural History Museum, Tring, UK (NHMUK); and the National Museum of Natural History (USNM, Smithsonian Institution), Washington DC. We measured the degree of phenotypic differentiation between each taxon using a system (elaborated in Tobias *et al.* 2010) in which an exceptional difference (a radically different coloration, pattern or vocalization) scores 4, a major character (pronounced difference in body part colour or pattern, measurement or vocalization) 3, a medium character (clear difference reflected by, e.g., a distinct *hue* rather than different colour) 2, and a minor character (weak difference, e.g. a change in shade) 1; a threshold of 7 is set to allow species status, species status cannot be triggered by minor characters alone, and only up to three plumage characters, two vocal characters (up to one spectral and one temporal), two biometric characters (assessed for effect size using Cohen's *d* where 0.2–2 is minor, 2–5 medium, 5–10 major and >10 exceptional) and one behavioural or ecological character may be counted. Where additional characters are apparent but under these rules cannot be scored, the formula 'ns[1]' is used, signalling 'not scored' but giving in parenthesis the estimated value of the difference in question. For morphometric analysis 10 male *lindenii*, *cyanolaemus* and *guerinii* were measured. *O. g. stubelii* is very rare in collections (we know of only eight specimens worldwide, distributed among five museums) and we could only measure one male (beard not fully developed) in AMNH (illustrated in Plates 1–3).

To investigate the conservation status of the taxa, we drew on appropriate literature sources and information from personal contacts and knowledge to assemble a general profile. Sound recordings were also collated from online and published sources and sonagrams produced using Raven Lite and compared subjectively.



**Plate 1.** Dorsal view of four taxa of *Oxygogon* (male specimens in AMNH): left to right *O. lindenii*, *O. guerinii*, *O. cyanolaemus* and *O. stubelii*.



**Plate 2.** Ventral view of same specimens as in Plate 1.



**Plate 3.** Lower bellies and tails of same specimens as in Plate 1.

## Results

### *Taxonomic status*

Each taxon differs from the other three principally in three or more of five plumage characters and one or two morphometric characters of males: the colour and length of the narrow backward-pointing crest, the colour of the narrow mesial 'beard', the colour of the crown-sides, the colour and pattern of the underparts, and the distribution of white (or in *stubelii* buff) in the tail (see Table 1), plus the length of bill, crest, wing and/or tail (see Table 2). From illustrations, texts and the evidence of the single male *stubelii* we examined, we presume this taxon to have the shortest crest of all the taxa. We assessed the strength of these characters as follows, with scores only given for differences between the taxon mentioned and all other taxa in the genus:

- a) The Santa Marta endemic form *cyanolaemus* uniquely has a (narrowly white-bordered) glittering purplish-blue beard (3); a dull greenish sheen on the crown-sides (2); brown-and-whitish mottled underparts (ns[1]); a white tail except for dark distal edges and central rectrices (3); a relatively short crest (Table 2; effect size *vs guerinii* 1.49, *vs lindeni* 4.23; score 1); and a shorter tail than the others (Table 2; effect size *vs next shortest guerinii* 2.32; score 2). Züchner (1999) mentioned buff-white on the outer rectrices but this is not apparent on material we examined; these feathers are white like much of the rest of the tail but with dark tips and an extremely thin dark line down the outside edge. Total 11.
- b) The form *lindeni* of the Venezuelan Andes uniquely has (apart from a few tiny green droplet-shaped spots on chin and throat) an all-white beard (3); blackish crown-sides (ns[1]); darkish brown underparts with relatively little pale scaling (1); no white in the tail except for white shaft-streaks on all but the central pair (3); a longer crest than other taxa (Table 2; effect size *vs cyanolaemus* 4.23, *vs guerinii* 3.086; score 2); and longer wings than the other taxa (Table 2; effect size *vs next longest cyanolaemus* 1.39; score 1). Its call differs from that of *stubelii* in note shape (score: ns[3]) (Fig. 1). Total 10.

c) The form *guerinii* of the East Andes uniquely has a (narrowly white-bordered) glittering green beard (3); purplish-sheened crown-sides (2); rather evenly scaled buff-and-mid-brown underparts (ns[1]); white centres to tail feathers (2); a relatively short crest (Table 2; effect sizes *vs lindeni* 3.086, *vs cyanolaemus* 1.49; score 1); and (apart from *stubelii*, which Table 2 hints might be very short-winged) shorter wings than the two preceding forms (Table 2; effect size *vs next shortest cyanolaemus* 1.06; score 1). Total 9.

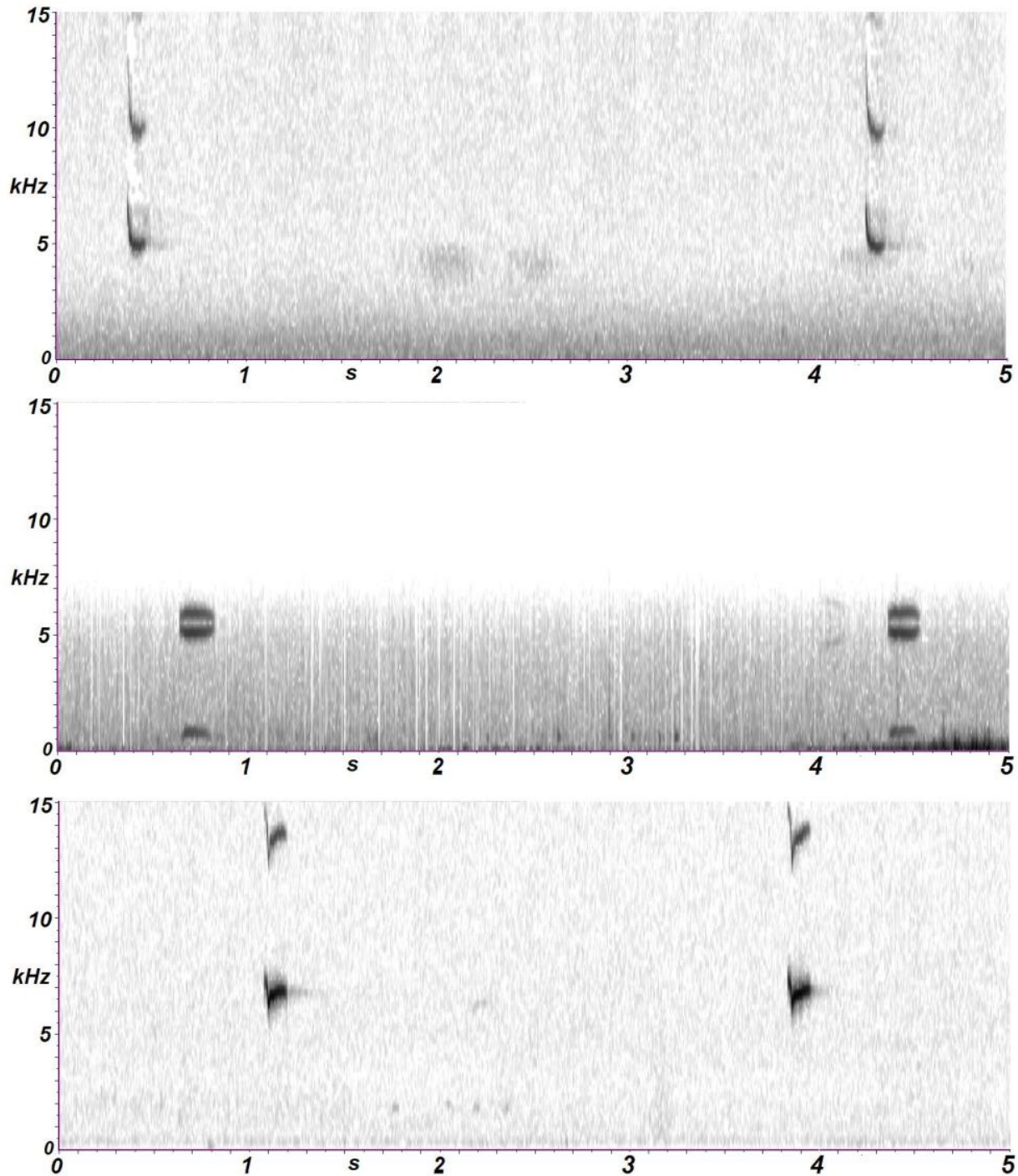
d) The form *stubelii* of the Central Andes uniquely has a tan and black crest (where the other three possess white and black feathers) (3); also a much shorter crest than other taxa (Table 1; allow at least 1); a short tan beard with green then purple reflectant spots centrally (3); buffy neck-sides (white in the other three taxa) and a buffier, brownish-tan belly (ns[1]); and a broad buffy-white line on the outer rectrix, with a buffy line around the shaft of the next two outer feathers (3). Fjeldså & Krabbe (1990) described the beard as 'coppery blue', but this is not apparent in any of the material we examined and is contradicted by Chapman (1917), who perceived green on the chin, and orange-purple in the longer plumes; but it can be seen in a photograph at a particular angle (p.51 in Mazariegos 2001). With respect to *lindeni*, this form also differs in the note shape of its call (Fig. 1) (score ns[3] *vs lindeni* but not scorable *vs others*). Total 10.

Females differ from each other mainly in possessing the same tail patterns as the males of their respective taxa but the crest is less prominent and beard less marked. All females of the genus have mixed white with a dull dark greenish-brown on the underparts, but each is slightly different in pattern from the other: *lindeni* is darkest below, with white largely confined to throat, breast and side-collar, with dark green-brown mottling; *cyanolaemus* is mottled green-brown and white throughout; *guerinii* has a slightly buff-shot white breast and its belly is less mottled, more uniform and a paler buff-brown (little if any green feathering); and *stubelii* has less white than the others, being an uneven rufous-buff or brownish-tan mixed with flecks of darker, vaguely greenish shades.

Notable apparent differences in vocalizations are linked to the morphological differences between *stubelii* and *lindeni*, giving further support for species rank. The only available sound recording of a typical call of *guerinii* is of an immature made with a camera (Fig. 1), which appears somewhat distorted so requires confirmation. The recording differs in the note shape (generally flat versus downstrokes or up-downstrokes) and lower acoustic frequency (Fig. 1) but it was not here compared to adult calls of other taxa for purposes of assessing rank. Contact calls of this population are also available (Álvarez *et al.* 2007), as are additional recordings of the main call of *stubelii* (Boesman 2012, Macaulay Library), but the small sample sizes and

incomplete taxon sampling do not allow for meaningful statistical comparisons to be made using sound recordings. In any case, the degree and significance of vocal learning in

hummingbirds are at an early stage of understanding (see, e.g., Gahr 2000, Araya-Salas & Wright 2013).



**Figure 1.** Sonagrams of: **Above:** *Oxygogon lindeni* (ML64920: P. Schwartz, Laguna de Mucubaji, Mérida, Venezuela, c. 08°48'N 70°48'W, 3,450 m). **Middle:** *Oxygogon guerinii* (XC37006: O. Cortes, Paramo de Sumapaz, Cundinamarca, c. 04°13'58"N 74°12'6"W; 3,200 m). **Below:** *Oxygogon stubelii* (XC101708: J. Minns, recorded perched on an *Espeletia* in paramo at entrance to Los Nevados National Park, above Manizales, Caldas, c. 04°56'00"N 75°21'0"W; 4,135 m).

**Table 1.** Distinctive characters of males of the four taxa in *Oxygogon*.

taxon	crest	beard	headside	underparts	tail
<i>cyanolaemus</i>	short, white	glossy purple-blue	dark green	brown-mottled whitish	white except tips & central pair
<i>lindeni</i>	long, white	white	velvet-black	(whitish-scaled) dark brown	bronzy throughout with white shafts
<i>guerinii</i>	medium, white	glossy green	purplish	(whitish-scaled) mid-brown	bronzy with broad white centres
<i>stubelii</i>	short, tan	tan, green, purple	blackish	brownish-tan	bronzy with buffy shaft-streaks & buff outermost vane

**Table 2.** Mean lengths (in millimetres) for four parameters in male *Oxygogon* hummingbirds (standard deviation in brackets).

taxon	n	bill	crest	wing	tail
<i>cyanolaemus</i>	10	14.2 (0.398)	22.6 (2.739)	71.2 (1.326)	54.8 (1.02)
<i>lindeni</i>	10	13.6 (0.31)	32.8 (2.031)	73.2 (1.588)	58.3 (1.107)
<i>guerinii</i>	10	13.5 (0.301)	26.3 (2.179)	69.9 (0.966)	57.2 (1.016)
<i>stubelii</i>	1	14.7	16.6	58.8	57.1

### Conservation status

*Oxygogon cyanolaemus* appears to be in serious danger. Of 62 *cyanolaemus* museum specimens logged by Project BioMap (Biomap Alliance 2013) the most recent were collected in 1946 by M. A. Carriker (23 specimens held in USNM). There appear to be no records of it since that time. In February 2007 Niels Krabbe undertook a brief survey of the paramo on the southern slope of the Santa Marta Massif for Fundación ProAves, but no *Oxygogon* was sound-recorded (Krabbe 2008) or reported (N. Krabbe *in litt.* 2007). Todd & Carriker (1922) noted that *cyanolaemus* was ‘found very sparingly’ and ‘very shy’, and also noted ‘Bushes and shrubbery are scarce on this paramo [Paramo de Mamarongo], hence the few birds found there’, possibly indicating habitat degradation. Strewé & Navarro (2004) found a pair of the very rare Santa Marta Wren *Troglodytes monticola* at high elevations on Santa Marta but did not record *Oxygogon*. Luna & Quevedo (2012) recently carried out surveys at higher elevations in the Santa Marta mountains, also encountering *T. monticola* and finding important populations of *Ramphomicron dorsale* in remaining patches of subparamo, but similarly did not record *Oxygogon*.

Considering that *cyanolaemus* may depend on *Espeletia* as possibly one of its most important food resources, it is to be noted that while the subtribe Espeletiinae includes about 126 species in 8 genera distributed across the paramos of the northern Andes, there is only one known species from Santa Marta, *Libanothamnus occultus*, recorded from subparamo to open slopes at 3,400–4,040 m across the massif (Cleef & Rangel 1984, Cuatrecasas 2013). Unfortunately, the paramo of the Sierra Nevada is seriously affected by extensive cattle herds belonging to indigenous communities, who repeatedly burn the paramos for pasture (WWF 2013). Cuatrecasas (2013) also noted that indigenous communities collected *L.*

*occultus* for firewood, which has further drastically reduced the population of this *fraijelon*.

N. Krabbe (*in litt.* 2007) and Luna & Quevedo (2012) noted that the widespread destruction of the paramo on Santa Marta gives serious cause for concern for species confined to high altitudes. The severe alteration of paramo, subparamo and adjacent elfin forest ecotones in the Sierra Nevada massif must have had a major impact on *Oxygogon cyanolaemus* and other taxa also restricted to this sensitive ecosystem, including *Troglodytes monticola*, *Leptasthenura andicola extima*, *Cistothorus platensis alticola*, *Phrygilus unicolor nivarius* and *Catamenia analis alpaca* (several of which have also not been recorded in decades).

The entire ranges of both *Libanothamnus occultus* and *Oxygogon cyanolaemus* fall within the Sierra Nevada de Santa Marta National Park, but given the intense pressure on the paramo there by indigenous peoples and also their direct use of the slow-growing *fraijelon*, this plant was officially registered in the Colombian Red List as Critically Endangered (B1a+b[iii]) (García *et al.* 2005). Clearly for the same reasons, especially given the likely dependence of the helmetcrest on the *fraijelon*, we judge that *Oxygogon cyanolaemus* also meets the IUCN criteria for Critically Endangered B1a+b(i,iii,v) and D:

- B. Geographic range in the form of B1 (extent of occurrence) estimated to be less than 100 km<sup>2</sup>, and (a) known to exist at only a single location (Sierra Nevada de Santa Marta National Park) and (b) projected decline in (i) extent of occurrence, (iii) area, extent and/or quality of habitat, and (v) number of mature individuals.
- D. Population size estimated to number fewer than 50 mature individuals.

This of course is potentially over-optimistic: we have no firm evidence that the species survives at all.

The other three species are evidently in a better situation, although their ranges are highly constrained. *Oxygogon lindeni* of western Venezuela has been reported to be 'seasonally very common in open paramo' (Hilty 2003) and 'the most abundant species [of bird] within its habitat, which is protected in two national parks (Sierra Nevada and Sierra La Culata), where recorded local densities are of at least 4–5 pairs/km<sup>2</sup>' (Züchner 1999).

*Oxygogon guerinii* of eastern Colombia appears to be common (see, e.g., Salamanca-Reyes 2011) and occurs in various national parks including Chingaza, Sumapaz and El Cocuy in the main East Andes. The genus was not, however, recorded in isolated paramos of Serranía de los Yariquíes (Donegan *et al.* 2010).

*Oxygogon stubelii* is only known from within the boundaries of the 583 km<sup>2</sup> Los Nevados National Park, around Nevado del Ruiz, but even in its preferred habitat it appears to be patchily distributed, not common and hard to find. Its estimated extent of occurrence is less than 400 km<sup>2</sup>, coincident with the superabundant stands of *Espeletia hartwegiana* across the paramos on the mountain range. Fortunately, threats are reasonably limited inside the park, which is well protected and an ecotourism destination. Nevertheless, the paramos continue to be burnt to provide fresh grasslands for cattle, while localised potato cultivation occurs in the subparamo. Based on available information, it is plausible that *O. stubelii* meets the IUCN criteria for Vulnerable D (<1,000 mature individuals). We recommend that researchers study *stubelii* to assess its population and determine potential threats.

We concur with Ridgely & Greenfield (2001) that an *Oxygogon* sight record from the Paramo de Angel in extreme north-west Ecuador (C. Mattheus in Fjeldså & Krabbe 1990) is best regarded as 'uncorroborated'.

## Discussion

In due course, vocal and molecular sampling may provide further evidence relevant to relationships between the four taxa of *Oxygogon*. However, it is remarkable that the extraordinary morphological distinctiveness of the four taxa has not been invoked until now to challenge the lumping of the taxa. It is indeed perplexing as to why these species were lumped in the first place, when many less distinctive hummingbirds were not so treated by Peters (1945), and applying standards similar to those invoked for *Oxygogon* to other genera would have resulted in large numbers of other congeners being lumped. The scoring system in Tobias *et al.* (2010) was calibrated according to levels of differentiation between acknowledged sympatric species pairs, and all four *Oxygogon* taxa greatly exceed the threshold of 7 set under this system for species rank, rising 2–4 points higher on the scale, emphasising their considerable divergence. These splits are largely based on comparative morphological

considerations, but are also supported in the case of *lindeni* versus *stubelii* at least by vocal differentiation. We therefore propose that the four taxa be returned to species rank, as they were afforded for example in Cory (1918) and earlier authors cited above.

The data on which this paper is based are being used in a forthcoming world list in which the English names proposed for the species are Blue-bearded Helmetcrest *Oxygogon cyanolaemus*, White-bearded Helmetcrest *O. lindeni*, Green-bearded Helmetcrest *O. guerinii* and Buffy Helmetcrest *O. stubelii* (del Hoyo & Collar in press). Cory (1918) and earlier authors used the English names Blue-throated, Linden's, Stübel's and Guerin's respectively for these species; but whilst reversion to earlier vernacular treatments, where possible, is a common approach, it seems unnecessary to resurrect patronyms for species in a group like this where morphological differentiation is so significant.

In many accounts of the species there is a brief reference to its habit of walking and hopping on the ground in search of insects and nectar. It is not clear how frequently this behaviour has been observed, but perhaps the first and seemingly the fullest report—albeit somewhat garbled in both his native Portuguese and his later English translation—is that of Ruschi (1972), who wrote of his encounter with *lindeni* (his English text here slightly cleaned of errors): 'It walks about the whole area, for more than half an hour... continuing to move in small jumps, at the maximum 5 centimeters from one side to another always moving forward and to the sides, capturing micro-insects and also looking for small quantities of nectar that it finds on a drop of dew of the crater of the tiny grass... this jumping walk is the only one known of the hummingbirds... besides this species the only species that perch on the ground are of the genera: *Chalcostigma* and they are only able to take a few paces, while *Oxygogon* makes great distances continually jumping.'

Ruschi (1972) then noted that an accompanying photograph (by C. Greenewalt) shows the bird's long legs and large feet relative to other species. If this habit therefore is common, particularly at times when taller plants are not flowering, it is perhaps possible that the species must sometimes be difficult to locate and evade capture in mist-nets. This possibility, while remote, offers a shred of hope that *O. cyanolaemus* may still survive somewhere in the paramos of the Sierra Nevada de Santa Marta. Although it has gone unrecorded for 67 years, there have been few high-elevation surveys in the Santa Marta mountains during this period and attention may not have been focused on the taxon owing to its subspecific status and reclusive feeding habits. A concerted endeavour is now urgently needed to undertake an exhaustive search for *O. cyanolaemus* and, if found, assess its chances of survival.

More broadly, the conservation of paramo in north-western South America is an increasingly urgent issue, owing to the degradation that follows human use of this habitat for agriculture and livestock production. It is well established

that paramo ecosystems provide crucial services of carbon storage and water filtration/provision (e.g. Buytaert *et al.* 2011, Cuatrecasas 2013). To mitigate the impact of livestock while retaining the social benefits of livestock production, it has been argued that grazing should be concentrated in certain areas, leaving others to recover their primary condition (Hofstede 1995). Whether such a model would work at this stage for the paramo vegetation in the Sierra Nevada de Santa Marta is not clear; but 50% of the 125 plants considered endemic to the massif are paramo species (Carbono & Lozano-Contreras 1997), and this in our view now renders an effective and equitable management system for such high levels of biodiversity imperative.

### Acknowledgements

We are most grateful to Paul Sweet (AMNH), Robert Prys-Jones (NHMUK) and Chris Milensky (USNM) for access to specimens in their care, and to Thomas Donegan for reviewing and providing various helpful comments on the manuscript as well as the sonagram and its interpretation.

### References

- Álvarez, M., Caro, V., Laverde, O. & Cuervo, A. M. 2007. *Guía sonora de los Andes colombianos*. Bogotá: Instituto Alexander von Humboldt, & Ithaca, NY: Cornell Laboratory of Ornithology.
- Araya-Salas, M. & Wright, T. 2013. Open-ended song learning in a hummingbird. *Biol. Letters* 23 (doi 10.1098/rsbl.2013.0625).
- BioMap Alliance (Darwin Initiative, Natural History Museum, Instituto de Ciencias Naturales de la Universidad Nacional de Colombia, Conservation International & Conservación Internacional Colombia) 2013. *Base de Datos Darwin: Proyecto BioMap base de datos de distribución de la avifauna Colombiana*. <http://www.biomap.net>.
- Boissonneau, A. 1840. Travaux inédits. *Revue Zoologique*, p. 7.
- Boesman, P. 2012. *Birds of Colombia MP3 sound collection*. Westernieland: Birdsounds.nl.
- Boucard, A. 1896. *The genera of hummingbirds being also a complete monograph of these birds*. London: Pardy & Son.
- Buytaert, W., Cuesta-Camacho, F. & Tobon, C. 2011. Potential impacts of climate change on the environmental services of humid tropical alpine regions. *Global Ecol. Biogeogr.* 20: 19–33.
- Carbono, E. & Lozano-Contreras, G. 1997. Endemismos y otras singularidades de la Sierra Nevada de Santa Marta, Colombia: posibles causas de origen y necesidad de conservarlos. *Rev. Acad. Colomb. Cienc.* 21: 409–419.
- Chapman, F. M. 1917. The distribution of bird-life in Colombia. *Bull. Amer. Mus. Nat. Hist.* 36.
- Cleef, A.M. & Rangel Ch., O. 1984. La vegetación del páramo del noroeste de la Sierra Nevada de Santa Marta. Pp.203–266 in T. van der Hammen & P. M. Ruíz, eds. *La Sierra Nevada de Santa Marta (Colombia), transecto Buritaca LaCumbre. Studies on Tropical Andean Ecosystems 2*.
- Clements, J. F. 1991. *Birds of the world: a check list*. Fourth edition. Vista, CA: Ibis Publishing Company.
- Clements, J. F. 2000. *Birds of the world: a checklist*. Fifth edition. Robertsbridge, U.K.: Pica Press.
- Clements, J. F. 2007. *The Clements checklist of birds of the world*. Sixth edition. Ithaca, NY: Cornell University Press (Comstock Publishing Associates).
- Cory, C. B. 1918. *Catalogue of birds of the Americas and the adjacent islands in the Field Museum of Natural History*, 2(1). Chicago: Field Museum of Natural History (Zool. Ser. XIII, Publication 197).
- Cuatrecasas, J. 2013. A systematic study of the subtribe Espeletiinae: Heliantheae, Asteraceae. New York: New York Botanical Garden Press (*Mem. New York Bot. Garden* 107).
- Dickinson, E. C., ed. 2003. *The Howard & Moore complete checklist of the birds of the world*. Third edition. London: Christopher Helm.
- Dickinson, E. C. & Remsen Jr, J. V., eds. 2013. *The Howard & Moore complete checklist of the birds of the world*, 1. Fourth edition. Eastbourne: Aves Press.
- Donegan, T. M., Avendaño, J. E., Briceño-L., E. R., Luna, J. C., Roa, C., Parra, R., Turner, C., Sharp, M. & Huertas, B. 2010. Aves de la Serranía de los Yariguíes y tierras bajas circundantes, Santander, Colombia. *Cotinga* 32: 72–89.
- Fjeldså, J. & Krabbe, N. 1990. *Birds of the high Andes*. [Copenhagen:] Zoological Museum, University of Copenhagen, and Svendborg: Apollo Books.
- Gahr, M. 2000. Neural song control system of hummingbirds: comparison to swifts, vocal learning (songbirds) and nonlearning (suboscines) passerines, and vocal learning (Budgerigars) and nonlearning (dove, owl, gull, quail, chicken) nonpasserines. *J. Comp. Neurology* 426: 182–196.
- García, N., Calderón Saenz, E. & Galeano, G. A. 2005. Frailejones (subtribu Espeletiinae, familia Asteraceae). *Libro Rojo Pl. Colombia 2*: 225–385.
- Gill, F. & Wright, M. 2006. *Birds of the world: recommended English names*. Princeton: Princeton University Press.
- Gould, J. 1887. *A monograph of the Trochilidae or family of humming-birds*. London: Henry Sotheran & Co.
- van der Hammen, T. & Cleef, A. M. 1986. Development of the high Andean paramo flora and vegetation. Pp.153–201 in F. Vuilleumier & M. Monasterio, eds. *High altitude tropical biogeography*. New York: Oxford University Press.
- Hartert, E. 1900. Trochilidae. In A. Reichenow, ed. *Das Tierreich: eine Zusammenstellung und Kennzeichnung der rezenten Tierformen*, 9. Berlin: Deutsche Zoologische Gesellschaft.
- Hilty, S. L. 2003. *Birds of Venezuela*. London: Christopher Helm.
- Hilty, S. L. & Brown, W. L. 1986. *A guide to the birds of Colombia*. Princeton: Princeton University Press.
- Hofstede, R. G. M. 1995. Effects of livestock farming and recommendations for management and conservation of

- páramo grasslands (Colombia). *Land Degradation & Development* 6: 133–147.
- del Hoyo, J. & Collar, N. J., eds. (in press) *The HBW/BirdLife International illustrated checklist of birds of the world*, 1. Barcelona: Lynx Edicions.
- del Hoyo, J., Elliott, A. & Sargatal, J. eds. 1999. *Handbook of the birds of the world*, 5. Barcelona: Lynx Edicions.
- Krabbe, N. 2008. *Birds of the Sierra Nevada de Santa Marta, Colombia* (sound CDs). San Jose, CA: John V. Moore Nature Recordings.
- Luna, J. C. & Quevedo, A. 2012. Primera fotografía en su habitat y nuevo avistamiento del Cucarachero de Santa Marta *Troglodytes monticola*, especie en peligro crítico. *Conservación Colombiana* 17: 31–32.
- Mazariegos H., L. A. 2001. *Hummingbirds of Colombia*. Second edition. Cali, Colombia: Luis A. Mazariegos H.
- McMullan, M., Donegan, T. M. & Quevedo, A. 2010. *Field guide to the birds of Colombia*. Bogotá: Fundación ProAves.
- Meyer, A. B. 1884. Über neue und ungenügend bekannte Vögel im Königlich Zoologischen Museum. *Zeitschr. gesammte Orn.* 1: 193–218.
- Meyer de Schauensee, R. 1948–1952. The birds of the Republic of Colombia. *Caldasia* 5(22): 251–380; (23): 381–644; (24): 645–871; (25): 873–1112; (26): 1115–1214.
- Meyer de Schauensee, R. 1966. *The species of birds of South America and their distribution*. Narberth, Penn.: Livingston Publishing Company for the Academy of Natural Sciences Philadelphia.
- Monroe, B. L. & Sibley, C. G. 1993. *A world checklist of birds*. New Haven and London: Yale University Press.
- Morony, J. J., Bock, W. J. & Farrand, J. 1975. *Reference list of the birds of the world*. New York: American Museum of Natural History (Department of Ornithology).
- Parzudaki, E. 1845. Nouvelle espèce d'oiseau-mouche [*Oniysmia (sic) lindeni*]. *Revue Zoologique* 8: 253.
- Peters, J. L. 1945. *Check-list of birds of the world*, 5. Cambridge, Mass.: Harvard University Press.
- Rauscher, J. T. 2002. Molecular phylogenetics of the *Espeletia* complex (Asteraceae): evidence from nrDNA ITS sequences on the closest relatives of an Andean adaptive radiation. *Amer. J. Bot.* 89: 1074–1084.
- Restall, R., Rodner, C. & Lentino, M. 2006. *Birds of northern South America: an identification guide*. London: Christopher Helm.
- Ridgely, R. S. & Greenfield, P. J. 2001. *The birds of Ecuador*. London: Christopher Helm.
- Ruschi, A. 1972. *Beija-flores (hummingbirds)*. São Paulo: Museu de Biologia 'Prof. Mello Leitão'.
- Salamanca-Reyes, J. R. 2011. Ecología de Barbudito de Páramo (*Oxygogon guerinii*, Trochilidae) en el Páramo de Siscunsi, Boyacá, Colombia. *Orn. Colombiana* 11: 58–75.
- Salvin, O. & Godman, F. D. 1880. On the birds of the Sierra Nevada of Santa Marta, Colombia. *Ibis* (4)4: 169–178.
- Sibley, C. G. & Monroe, B. L. (1990) *Distribution and taxonomy of birds of the world*. New Haven: Yale University Press.
- Stattersfield, A. J., Crosby, M. J., Long, M. J. & Wege, D. C. 1998. *Endemic bird areas of the world: priorities for biodiversity conservation*. Cambridge, U.K.: BirdLife International (Conservation Series 7).
- Stotz, D. F., Fitzpatrick, J. W., Parker III, T. A. & Moskovits, D. K. 1996. *Neotropical birds: ecology and conservation*. Chicago: University of Chicago Press.
- Strewe, R. & Navarro, C. 2004. New and noteworthy records of birds from the Sierra Nevada de Santa Marta region, north-eastern Colombia. *Bull. Brit. Orn. Club* 124: 38–51.
- Tobias, J. A., Seddon, N., Spottiswoode, C. N., Pilgrim, J. P., Fishpool, L. D. C. & Collar, N. J. 2010. Quantitative criteria for species delimitation. *Ibis* 152: 724–746.
- Todd, W. E. C. & Carriker Jr., M. A. 1922. The birds of the Santa Marta region of Colombia: a study in altitudinal distribution. *Ann. Carnegie Mus.* 14: 1–611.
- Wolters, H. E. 1975–1982. *Die Vogelarten der Erde*. Hamburg: Paul Parey.
- WWF 2013. = <http://worldwildlife.org/ecoregions/nt1007>
- Züchner, T. 1999. Bearded Helmetcrest *Oxygogon guerinii*. Pp.648–649 in J. del Hoyo, A. Elliott & J. Sargatal, eds. *Handbook of the birds of the world*, 5. Barcelona: Lynx Edicions.